COMPARISON OF THE DIPLOPOD COMMUNITIES BEFORE AND AFTER AN EXCEPTIONAL DROUGHT IN THE FOREST OF ORLEANS (FRANCE)

BY

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Summary: A fairly severe drought occured in the Forest of Orleans in the Autumn of 1985. Its effects on Diplopoda are studied by comparing the communities of eight stations in the Springs of 1985 and 1986. Among the six most abundant species, the density remains stable in four but decreases significantly in two Craspedosomatida.

The species' resistance to drought is discussed in connection with experimental data in literature and with their distribution in dry or humid habitats.

Diplopoda, like soil fauna in general, were long regarded as hygrophilous and incapable of withstanding a long drought, but that generalization was somewhat arbitrary (Vannier, 1970). Actually, a number of ecophysiological studies have made it possible to measure resistance to desiccation of Diplopoda in experimental conditions, and the results are very variable from one species to another (Perttunen, 1953; Barlow, 1957; Haacker, 1968; O'Neill, 1969; Stewart & Woodring, 1973; Wegensteiner, 1982; Meyer & Eisenbeis, 1985). The comparison between species' resistance to desiccation and their natural distribution has now given weight to the idea that a relationship exists between water balance and habitat in most land Arthropoda, dry habitats being occupied by desiccation-resisting species and humid habitats by non-resisting ones, notably in Diplopoda (Edney, 1977; Wegensteiner, 1982; Meyer & Eisenbeis, 1985).

A fairly severe drought occurred in the centre of France in the early Autumn of 1985, when a study of the diplopod communities in the Forest of Orleans was just beginning. Although, owing to the unpredictability of this drought, it has not been possible to measure its full effects on the soils, some interesting observations have been made on the resistance of species in natural conditions. Moreover, the validity of the relationship between this resistance and the type of habitat has been studied.

THE SITE AND ITS CLIMATE

The Forest of Orleans is a mosaic of deciduous, coniferous and mixed stands. The eight stations dealt with in this study belong to the Ingrannes Massif (13 600 ha), and some of their features are shown in table 1. The substratum consists of sand and clay of Sologne, and the soils usually comprise a shallow, impermeable layer, which is the floor of a temporary water table (pseudogley). The depth of this water table has been measured with three piezometers per station for one year, and it comes more or less up to ground level from November to June. As a water table can supply overlying soil with water by capillary attraction—up to 40 cm in sand and more than 1m in clay (Duchaufour, 1984)—this strongly influences the soil moisture in the Ingrannes Massif for more than half the year. Taking into account the depth of the water table and the texture of the soil, stations Nos. 1 and 4 are the most humid and station No. 8 is the driest (table 1).

Station No.	Stand nature	Upper soil texture	Mean depth of water table (cm) (Dec. to Jun.)	Soil moisture
1	Deciduous	Clay	37	+ +
2	Deciduous	Sandy silt	55	+ -
3	Deciduous	Silty sand	64	+ -
4	Coniferous	Silty sand	37	+ +
5	Coniferous	Sand	56	+ -
6	Mixed	Silty sand	62	+ -
7	Mixed	Silty sand	57	+ -
8	Mixed	Sand	77	- -

(+ + : often waterlogged; + -: more or less humid but not waterlogged; -- dry)

Tab. 1. Some features of the eight stations in the Forest of Orleans

The climate of the Orleans region, still under the influence of the Atlantic Ocean, is rather humid as shown in the ombrothermic diagram of Gaussen (1955) (fig. 1): a month would be considered dry if rainfall were less than 2mm/°C/month, i.e. if the rainfall curve were below the curve of mean monthly temperatures in the diagram. Nevertheless, the climatic water budget, i.e. the difference between rainfall (R) and potential evapotranspiration (PE) (Thornthwaite & Mather, 1955), shows a deficit in summer. That creates a relative dryness every year, during which water tables disappear, and there is a tendency for soils to become

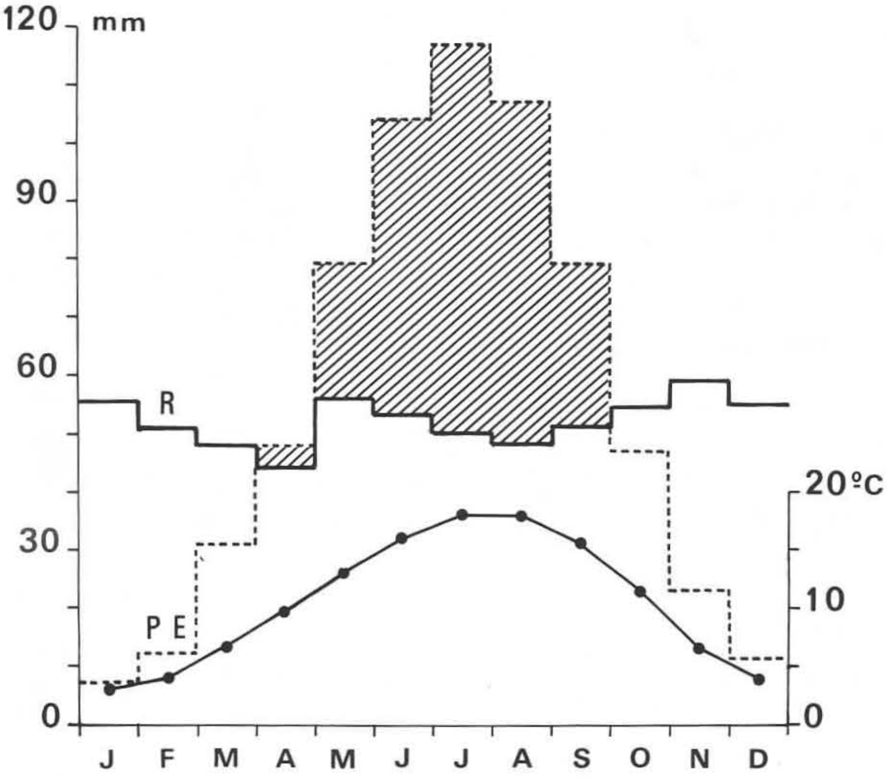

Fig. 1. Regional climatic data (Orleans, averages from 1951 to 1980): rainfall (R), potential evapotranspiration (PE) and mean monthly temperature. The shaded area corresponds to climatic water deficit.

drier and drier until September in spite of precipitations (Vannier, 1972).

If the actual climate over recent years is now considered, an exceptional drought appeared early in the Autumn of 1985 (fig. 2). The cumulative total of the climatic water deficit, which was 198 mm in October 1983 and 217 mm in August 1984, reached 335 mm in October 1985, i.e. 103 mm above normal in the region. There is no doubt that such a water shortage in late Summer—a critical period—resulted in a considerable soil moisture deficit. Its exact extent is not known, for soil water budget depends on real evapotranspiration (RE), which is quite close to PE in forest but varies according to many factors, such as tree species and stand density (Aussenac, 1980). The actual deficit also depends on the initial soil moisture storage (field capacity), which varies from one station to another. But, even if the field capacities are high and

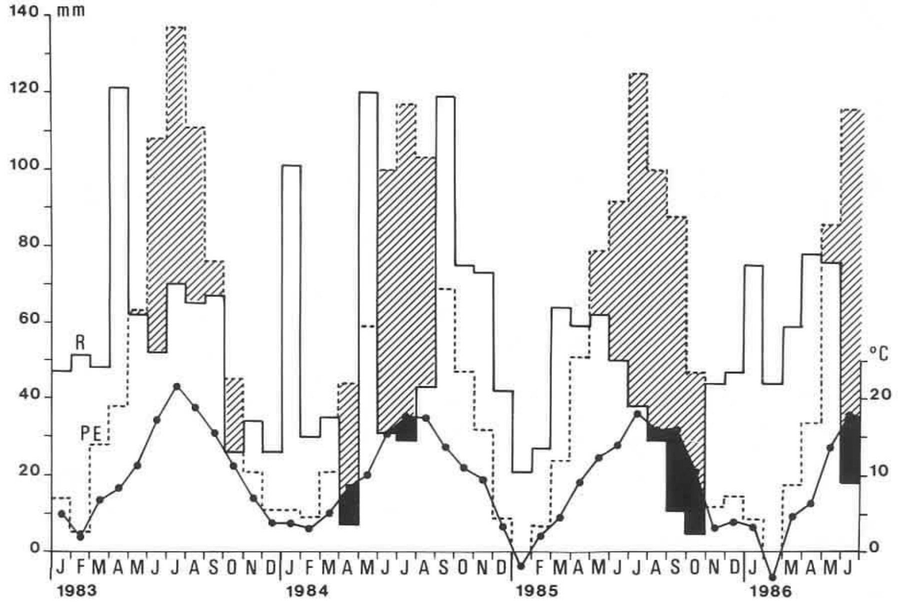

Fig. 2. Local climatic data (Ingrannes Massif) from 1983 to 1986: rainfall (R), potential evapotranspiration PE and mean monthly temperature. The shaded area corresponds to climatic water deficit. Dry months in Gaussen's sense are shown in black.

RE relatively low, it is clear that soils underwent a severe moisture deficit for at least two months, in September and October 1985.

The soil fauna of the Forest of Orleans is obviously adapted to the relative dryness which periodically occurs every Summer. But the duration and, consequently, the severity of the drought in 1985 make it an *aperiodical* phenomenon in the sense of Mondchasky (1958), against which there is no biological pre-adaptation. Its effects on Diplopoda are considered by comparing the communities of the eight stations quantitatively in the Springs of 1985 and 1986.

THE SAMPLING PROCEDURE AND THE RESULTS

In each station, sampling units are taken at random in a 400m^2 area. Each unit includes litter (Ao) and an upper soil layer (A1) in a 1/16m^2 quadrat, and rotting wood more than 1,5 cm thick in a 1 m^2 quadrat. Diplopoda are extracted by Tullgren funnels 25 cm in diameter. The eight stations are sampled in the Spring of 1985 (4 Apr. to 12 Jun.), in the Autumn of 1985 (11 Oct. to 12 Dec.) and in the Spring of 1986 (18

	Spring 1985	Autumn 1985	Spring 1986
Number of sampling units	62	48	48
Overall density (Ind./m^2) (± standard error)	115 (± 28)	141 (± 48)	102 (± 38)
Number of species	12	13	13
Relative frequency (%)			
Iulida			
Cylindroiulus nitidus (Verhoeff, 1891)	6	6	5
Cylindroiulus londinensis (Leach, 1814)	2	0.9	4
Cylindroiulus punctatus (Leach, 1814)	0.5	0.9	0.3
Leptoiulus bruyanti Ribaut, 1951	0.2	0.5	0
Tachypodoiulus niger (Leach, 1815)	1	0.9	0.7
Ommatoiulus sabulosus (Linné, 1758)	0	0	0.3
Craspedosomatida			
Chamaesoma brolemanni Ribaut & Verhoeff, 1913	25	1	2
Melogona gallica (Latzel, 1884)	11	3	2
Chordeuma sylvestre C.L. Koch, 1847	0.7	0.5	0.7
Glomerida			
Glomeris marginata (Villers, 1789)	3	9	7
Glomeris hexasticha Brandt, 1834	1	2	2
Polydesmida			
Polydesmus angustus Latzel, 1884	6	7	4
Polyzoniida			
Polyzonium germanicum Brandt, 1831	43	65	72
Polyxenida			
Polyxenus lagurus (Linné, 1758)	0	4	1
Diversity index (bits)	2.36	2.01	1.75

Tab. 2. Variations of the overall density of Diplopoda and of the relative frequency of species from the Spring of 1985 to the Spring of 1986 (eight stations taken as a whole)

Apr. to 13 Jun)[1]. The number of sampling units is the same in each station, with one exception: eight in the Spring of 1985 (except station No. 7 with six), six in the Autumn of 1985 and six in the Spring of 1986.

Abundances are compared in the eight stations taken as a whole. The Spring sample of 1985, representative of eight communities in various ecological conditions *before the drought*, is compared with the Autumn sample of 1985 and the Spring sample of 1986, representative of *the same communities after the drought*. The results appear in table 2. They show that the overall density of Diplopoda is not very altered by the drought, as it only decreases from 115 Ind./m^2 in the Spring of 1985 to 102 Ind./m^2 in the Spring of 1986 (the difference is not significant). The Autumn density, representing mainly the post-drought period, is not significantly different from Spring densities, though slightly higher. This trend is logical because most species have younger, and therefore more numerous individuals in Autumn than in Spring; this is particularly the case of the most abundant one, *Polyzonium germanicum*, which breeds in Summer (David & Couret, 1985); only annual Craspedosomatida are always more numerous in Spring than in Autumn (David, 1984).

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[1] In fact, twelve stations were sampled in the Autumn of 1985 and Spring of 1986, but only eight previously sampled in the Spring of 1985 have been retained here for comparative purposes.

	Spring 1985	Spring 1986	Difference
P. germanicum	50	73	+ 23 (N.S.)
C. brolemanni	29	2	-27 ($p<0.05$)
M. gallica	13	2	-11 ($p<0.01$)
C. nitidus	7	5	-2 (N.S.)
P. angustus	6	4	-2 (N.S.)
G. marginata	3	7	+ 4 (N.S.)

Tab. 3. Variations of the density (Ind./m^2) of the six most abundant species, from the Spring of 1985 to the Spring of 1986 (eight stations taken as a whole)

However, if the overall density does not vary much, the survey of table 2, species by species, shows some important changes. *P. germanicum*, the most abundant species in 1985, ranks first again in 1986, but its relative frequency increases from 43% to 72%. The species which rank second and third in 1985, *Chamaesoma brolemanni* and *Melogona gallica*, drop to sixth place in 1986, from 25% and 11% respectively to 2%. These changes can be summarized with a diversity index, such as that of Shannon, which decreases greatly from the Spring of 1985 (2,36 bits) to the Spring of 1986 (1,75 bits): the fall of the index indicates the extent of the concentration in favour of the stress resisting species (*P. germanicum*), and at the expense of both the Craspedosomatida.

The comparison of the density of the six most abundant species, between the Springs of 1985 and 1986, appears in table 3. Statistical tests indicate that it significantly decreases in *C. brolemanni* and *M. gallica*. In the other four species, variations are not significant—particularly in *P.*

germanicum, whose spatial dispersion is very contagious—and it can only be concluded that density seems stable.

Finally, it must be emphasized that Diplopoda do not resettle in rotting wood, where a very small proportion of the communities live (about 1%) in 1985 as well as in 1986.

Conclusions and discussion

The question whether the soil moisture deficit of the Autumn of 1985 has had an impact on Diplopoda has no general answer. Among the six most abundant species, four have kept stable densities and do not seem to have been affected by the drought, whereas densities have decreased significantly in the other two.

The resistance of the first four species (*P. germanicum, Glomeris marginata, Cylindroiulus nitidus* and *Polydesmus angustus*) can be explained in two ways:

— the water availability limit has not been reached. Indeed, Vannier (1970, 1973) showed that water is still available for soil fauna at low moisture contents. The availability limit varies according to species and stadium, but it may be very low (pF = 5 for Oribatid mites) and until this threshold is reached, animals seem insensitive to moisture changes.

— the water availability limit has been reached, but these four species are fairly well adapted to conserving water by restricting losses.

Only the densities of *C. brolemanni* and *M. gallica* have significantly decreased. This could be due to factors other than the drought, for it must be emphasized that the results come from an observation and not from an experiment: there are no means of knowing how the density would have varied without the drought. However, a negative effect of the low temperatures in February 1986 is unlikely, because a cold wave took place before in January 1985, apparently without any consequences. The effect of other factors is purely hypothetical. On the other hand, the assumption that the drought has been the determining factor in the sudden modifications of the two species dynamics is corroborated by the fact that Craspedosomatida are always among the least desiccation-resisting species in laboratory experiments (Haacker, 1968; O'Neill, 1969; Meyer & Eisenbeis, 1985). Thus, the observations made in the Forest of Orleans are a life-size illustration of the sensitivity to dryness in the species belonging to this Order.

A second question worthy of discussion is whether it is possible to establish a relationship between species' habitat and their resistance to drought, for instance in the six most abundant species. Do the ones which resist best live mainly in dry places, and the others in humid? Their

Station No.	1	4	2	3	5	6	7	8
Soil moisture	+				+ –			––
Probability for								
P. germanicum	–	**0.58**	–	0.06	0.11	0.22	0.03	–
C. brolemanni	**0.92**	–	0.07	–	–	0.01	–	–
M. gallica	–	0.11	–	**0.48**	–	0.23	0.18	–
C. nitidus	– –	–	0.21	**0.79**	–	–	–	–
P. angustus	0.06	0.21	**0.32**	0.15	0.01	0.12	0.05	0.08
G. marginata	–	0.01	**0.68**	0.06	0.01	0.18	–	0.06

Tab. 4. Probabilities of collecting the six most abundant species in each of the stations

(+ + : often water logged; + – : more or less humid but not water logged; ––: dry)
(highest probability in **bold**)

distribution in the different stations is given in a conditional probability table (table 4). In determining in which of the eight stations each species has the highest probability of being collected, it is established that *C. brolemanni*, which can be regarded as having a very low resistance to drought, is actually concentrated in a very humid station (No. 1), often waterlogged in Winter and drying slowly in Summer because of its excess clay. But *M. gallica*, another low-resistance species, do not occupy the most humid stations. Moreover, *P. germanicum*, known to live in very humid places (Schubart, 1934; Wegensteiner, 1982)—confirmed in the Forest of Orleans by its maximum abundance in station No. 4—proved its resistance to drought, at least more than Craspedosomatida. Consequently, if it is true that many examples point to a correlation between the water balance of a species and its habitat (Edney, 1977), there are also many exceptions. From a theoretical point of view, this was foreseeable insofar as one single factor cannot account for species distribution. In the case of Diplopoda alone, *Iulus scandinavius* in the Netherlands has a low resistance, but its range resembles that of the very resistant *Ommatoiulus sabulosus* (Barlow, 1957); in Germany, Haacker (1968) finds a difference between resistance to desiccation and habitat in several species (*Cylindroiulus latestriatus*, *Tachypodoiulus niger*). The case of *P. germanicum* is another very interesting exception: Wegensteiner (1982) considers that this species should not need protection against transpiration, since it is so well-adapted to occupying humid sites. Yet it is quite well-protected, unless it can obtain water at high pF. Perhaps it is protected against desiccation by its very adaptation to waterlogged habitats. Indeed, a land species frequently living in contact with water probably needs to protect itself against *an excess of external water* and, as impermeabilities can operate both ways, that may confer effective resistance to desiccation in case of need.

In conclusion, the drought in the Autumn of 1985 in France showed that the least resistant Diplopoda are not necessarily the most hygrophilous, but merely those which have not acquired a protective system in the course of their evolution, like most Craspedosomatida. Obviously, the small size of these species goes against them. In an exceptional situation, of a catastrophic nature, they are exposed to fast-killing desiccation, and their long-term survival implies compensating advantages, such as a high rate of increase when conditions return to normal.

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